pollinating species. X. Variation in natural populations of Avena fatua and A. barbata. Amer. Naturalist 101:19–33.

Kearney, T. H., and R. H. Peebles. 1951. Arizona flora. Univ. California Press, Berkeley.

Knowles, P. F. 1943. Improving an annual brome grass, Bromus mollis L. for range purposes. J. Amer. Soc. Agron. 35:584–594.

Lewontin, R. C. 1965. Selection for colonizing ability. *In* H. G. Baker and G. L. Stebbins (eds.), The genetics of colonizing species. Academic Press, New York.

Morley, F. H. W. 1958. The inheritance and ecological significance of seed dormancy in subterranean clover (Trifolium subterraneum L.). Austral. J. Biol, Sci. 11:261–274.

Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.

Raven, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289–347.

Sagar, G. R., and J. L. Harper. 1960. Factors affecting the germination and early establishment of Plantains (Plantago lanceolata, P. media and P. major). *In* J. L. Harper (ed.), The biology of weeds. Blackwell, Oxford.

Stebbins, G. L. 1965. Colonizing species of the native California flora. *In* H. G. Baker and G. L. Stebbins (eds.), The genetics of colonizing species. Academic Press, New York.

Thorne, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1–77.

Weil, J., and R. W. Allard. 1965. The mating system and genetic variability in natural populations of Collinsia heterophylla. Evolution 18:515–525.

THE POLYPODIUM VULGARE COMPLEX IN THE PACIFIC NORTHWEST

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Introduction

The *Polypodium vulgare* complex in the Pacific Northwest has been a problem to taxonomists since a number of names have been applied to ill-defined and inadequately understood taxa. In 1961 the author began a critical study of this complex in northwestern North America using modern biosystematic methods in an effort to clarify the taxonomic situation and if possible to elucidate the evolution of the complex (Lang 1965). The basic findings of this paper have recently been briefly summarized by Taylor (1970). A more detailed discussion is presented here to further clarify the taxonomy and evolution of the complex in the Pacific Northwest.

As defined here, northwestern North America comprises the area from Alaska south along the Pacific Coast to central California and east to the Rocky Mountains. Although most of the populations of the complex examined here were from this area, a number of herbarium specimens from elsewhere in western North America were also studied.

The specimens examined in this study were from UBC, UC, US, V, WS, and WTU. A complete list of specimens examined is available from the author on request.

The genus *Polypodium* in this geographical area centers around two princple groups: one is represented by *P. glycyrrhiza* D. C. Eaton, the other by *P. hesperium* Maxon. At their morphological extremes these two taxa are distinct; but they are so variable that their boundaries are often blurred, and it is often difficult to distinguish them using the classical characteristics of frond size and frond segment shape.

In central California, *P. californicum* Kaulf. and *P. glycyrrhiza* are apparently closely related (Lloyd and Lang, 1964; Lloyd, 1962). *Polypodium scouleri* Hook. & Grev., distinctive in its morphology and geographical distribution, raises no taxonomic problems. The eastern North American *P. virginianum* L. known also from northeastern British Columbia and the Yukon, is considered only as it relates to *P. hesperium.* These three species appear to have played no immediate role in the evolution of the *P. hesperium-glycyrrhiza* complex.

POLYPODIUM HESPERIUM-GLYCYRRHIZA COMPLEX

As far as can be determined, the European species of the *P. vulgare* complex, as delimited by Shivas (1961a; 1961b), *P. vulgare* L. sens. strict., *P. australe* Fée, and *P. interjectum* Shivas, are not present in my study area.

During the course of the investigation, an interesting problem was discovered concerning those forms centering about *P. hesperium* Maxon. Typically, any *Polypodium* from western North America, with short blunt frond segments has been considered to be *P. hesperium.* As previously reported, there are two cytotypes within *P. hesperium,* a diploid $n = 37$, (Manton, 1950; Evans, 1963) and a tetraploid $n = 74$ (Knobloch, 1962; Lloyd, 1963). These reports are from geographically widely separated populations, the tetraploids from Arizona, the diploids from Washington and Oregon. Cytological investigations of populations of *Polypodium* from British Columbia have shown that both cytotypes of *P. hesperium* are present and that *P. glycyrrhiza* is uniformly diploid.

Further study of the tetraploid and diploid cytotypes of *P. hesperium* revealed that there were other differences between them in addition to geographical distribution and cytology. These differences are summarized in Table 1 along with the distinguishing features of *P. glycyrrhiza* and *P. virginianum.*

It is felt that the differences between the two cytotypes usually included in *P. hesperium* sens. lat. are such as to warrant their recognition as two distinct species. The name *Polypodium montense* Lang was proposed for the diploid cytotype formerly included in *P. hesperium* sens. lat. (Lang, 1969).

TABLE 1. CHARACTERS DISTINGUISHING POLYPODIUM GLYCYRRHIZA P. HESPERIUM, P. MONTENSE, AND P. VIRGINIANUM

	P. glycyrrhiza	*P. hesperium*	*P. montense*	*P. virginianum* sens. lat
Chromosome No.	n = 37	n = 74	n = 37	n = 37, n = 74
Frond shape	oblong to ovate	oblong	oblong	oblong-triangular
Segment shape Index (mean)	1.65	2.72	2.99	....
Segment shape	acuminate to acute	acute to obtuse	obtuse	acute
Sorus shape	circular	oval	circular	circular
Sorus location	median	median	submarginal	submarginal
Paraphyses	absent	very rare	common	common
Rhizome taste	licorice	licorice	acrid	acrid
Scale stripe	absent	absent	+ —	present
New fronds	autumn	summer	spring	summer
Geographical distribution	coastal	interior	western mountains	eastern N. America

The examples of Manton (1950) and Shivas (1961a; 1961b) in considering the cytotypes of the *P. vulage* complex as distinct species have been followed here. As in the European ones the northwest North American cytotypes display the fundamental characteristics of distinct natural taxa. They appear to be reproductively isolated, possess distinctive geographical and ecological distributions, and can be distinguished morphologically, although admittedly not always with ease.

Table 2 indicates the synaptic chromosomal association at diakensis in these plants and the source of the material. The tetraploid populations of *P. hesperium* are from the interior of British Columbia while the diploids, *P. montense,* are from the coastal mountains. Figures 3g, 4f, and 5f show diakinesis in both cytotypes of *P. hesperium* and *P. glycyrrhiza.*

When it was discovered that both the tetraploid and diploid cytotypes were present in British Columbia, a search was made for possible triploid hybrids in areas where all three cytotypes, the two o*f P. hesperium* and that of *P. glycyrrhiza,* might be sympatric. A search of the Fraser River Canyon and Cheakamus River regions of British Columbia yielded two morphologically distinct triploid hybrids (fig. 6, 7). At metaphase I of meiosis both triploids showed 37 bivalents plus 37 univalents. Mature sporangia contained aborted spores varying in size and degree of malformation. The aborted spores appeared to be similar to those described by Wagner and Chen (1965) in hybrid *Dryopteris.* The significance of these hybrids will be discussed later.

THE DIFFERENCES BETWEEN P. GLYCYRRHIZA, HESPERIUM, AND MONTENSE

In addition to Table 1, more information concerning the differences between these three species is provided by the species descriptions in the systematic treatment and the illustrations, Figs. 3, 4, and 5. It is neces-

TABLE 2. CHROMOSOME NUMBERS IN POLYPODIUM IN NORTHWEST NORTH AMERICA

Collections (UBC) are from British Columbia unless otherwise noted. Collection numbers are those of Lang, unless otherwise noted. Meiotic association and/or diploid number are given.

P. hesperium. 74_{II}, Clearwater, *70, 112*; 74_{II}, **$2n = 148$**, Clearwater, *71, 111, 114*; 74_{II}, **$2n = 148$**, Craigellachie, *73*; 74_{II}, **$2n = 148$**, Wigwam, *74;* 74_{II}, **$2n = 148$**, Kootenay Bay, *Bosorowich* s.n.; **$2n = 148$**, Alta Lake, *212*; **$2n = 148$**, Marblehead, *Taylor* & *Szczawinski 610*; 74_{II}, Cambie, *Taylor* & *Szczawinski 442*; 74_{II}, Lake Chelan, Washington, *130, 138.*

P. montense. 37_{II}, Mt. Seymour, *96, 218*; 37_{II}, near Cheekeye, *117C2*; 37_{II}, Yale, *120, 118*; **$2n = 74$**, McGuire, *211*; **$2n = 74$**, Garibaldi, *214*; 37_{II}, Alexander Bridge, Fraser R., *122-6.*

P. glycyrrhiza. 37_{II}, Troutdale, Oregon, *188, 189*; 37_{II}, Crown Pt., Columbia River Gorge, Oregon, *190, 192*; 37_{II}, Queen Charlotte Islands, *24, 26, 28, 30, 33;* 37_{II}, Terrace Bridge, *53;* 37_{II}, *Squamish, 221;* 37_{II}, Howe Sound, *222, 223;* 37_{II}, Pitt River, *216, 217*; 37_{II}, Cheekeye, *106*; **$2n = 74$**, Garibaldi Station *213.*

P. hesperium × *montense.* $37_{II} + 37_{I}$, Alexander Bridge, Fraser River, *122-3.*

P. glycyrrhiza × *hesperium.* $37_{II} + 37_{I}$, **$2n = 111$**, Alexander Bridge, Fraser River, *125-2*; **$2n = 111$**, Green River, *210C.*

TABLE 3. SUMMARY OF FROND MEASUREMENTS OF POLYPODIUM GLYCYRRHIZA, P. HESPERIUM, AND P. MONTENSE

	Blade length	Blade width	Stipe length	Segment length	Segment width	Ratio seg. l/w	Segment tip index
			P. glycyrrhiza				
N	325*	354	375	339	287	349	210
Observed range	20–470	14–156	11–340	7–85	3–11	1.8–12.00	1.0–3.0
Mean	172.6	60.30	93.56	33.28	6.65	5.6	1.65
80% obs.**	69–280	35–92	36–143	18–53	5–8	3.3–7.4	....
			P. hesperium				
N	199	171	223	218	215	284	206
Observed range	30–265	12–83	12–155	9–45	5–11	1.3–3.8	1.5–3.0
Mean	114.09	33.29	56.75	17.64	7.25	2.44	2.72
80% obs.**	63–189	22–48	28–100	11–25	6–9	1.9–3.1	....
			P. montense				
N	216	224	213	221	220	315	217
Observed range	18–190	11–45	8–142	5–25	3–12	1.2–3.6	2.0–3.0
Mean	80.58	23.58	57.94	12.92	5.60	2.35	2.99
80% obs.**	46–122	17–30	28–100	9–17	4–7	1.8–3.0	....

* All measurements in mm.

** The two extreme values between which 80 per cent of the observations fell.

sary here, however, to comment on some of the more important differences and to discuss some of the salient features that might be indicative of the relationships of the taxa.

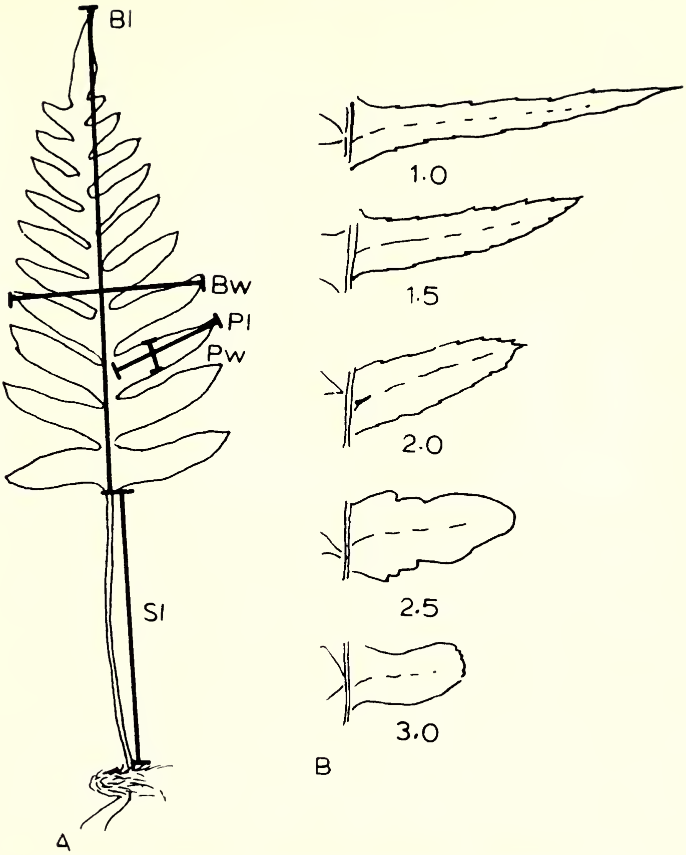


Fig. 1. Quantitative measures made on *Polypodium*: a, linear measurements, Bl—blade length, Bw—blade width, Pl—pinnae length, Pw—pinnae width, and Sl—stipe length; b, numerical index for expressing the shape of the frond segments (see text for explanation).

Figure 1a shows the frond measurements that were taken to circumscribe the variation in the size of the fern. As seen in Table 3, the three species of *Polypodium* from the Pacific Northwest are difficult to separate using the quantitative characters of blade length, blade width and stipe length because of the overlap in size range. The shape of the frond segment has often been used as a diagnostic character to distinguish between *P. glycyrrhiza* and *P. hesperium* sens. lat. To quantify the shape of the frond segments, an arbitrary index was assigned to the range of shapes found in the *P. vulgare* complex in the Northwest. The most attenuated segments were assigned 1.0 with 0.5 steps given to intermediate shapes up to 3.0 for the most obtuse frond segments. Figure 1b shows the shapes and the numbers assigned to them. Specimens of *P. glycyrrhiza, P. hesperium,* and *P. montense* were examined and the shape

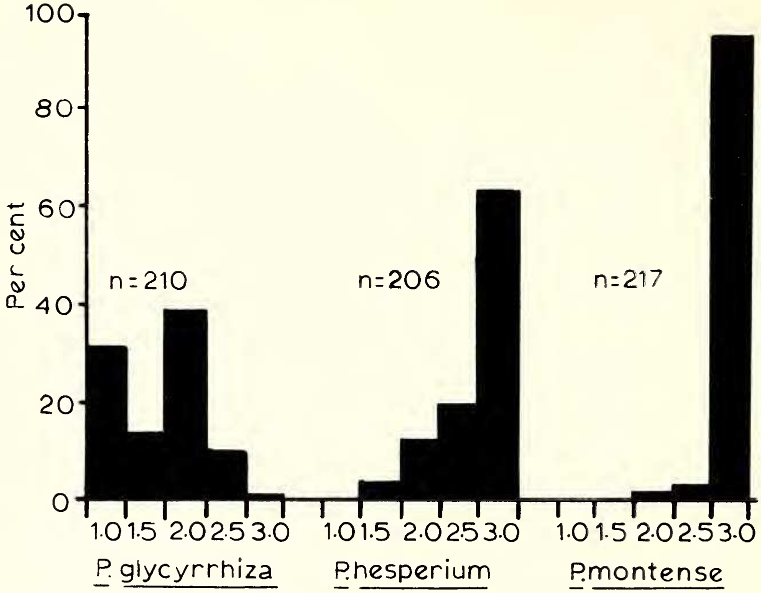


FIG. 2. Distributions of the numerical index of segment shape expressed as per cent of total in *P. glycyrrhiza, P. montense,* and *P. hesperium.*

index for each plant determined. The results of this study (fig. 2) show the great overlap between *P. montense* and *P. hesperium.* This overlap in the 3.0 range (obtuse segments) may be one reason why the diploid *P. montense* remained undetected among the plants of tetraploid plants of *P. hesperium.*

The morphology of epidermal cells has recently proved to be valuable in taxonomic and evolutionary studies of the pteridophytes (Blasdell, 1963; Wagner, 1954; Evans and Wagner, 1964). Although epidermal morphology does not provide any clear diagnostic characters for distinguishing members of the *P. vulgare* complex, these cells do exhibit patterns which are useful in assessing relationships among the taxa when other evidence is also considered.

The shape of the epidermal cells differs in the lower and particularly the upper epidermis among the species. The upper epidermal cells in *P. hesperium* (fig. 3c) are more or less intermediate between the two diploids (compare fig. 4c–5c). At the tips of the free vein ends of the fronds, on the upper surface, there are structures that appear to be hydathodes (figs. 3e, 4e, 5e). In *P. montense* these structures are frequently smaller and composed of fewer cells than those of the other two species.

The guard cells of the lower epidermis of *P. hesperium* seem to be larger (usually more than 24 μ long) and fewer in number per square millimeter (average ca. 35 per mm^2) of leaf surface than those of *P.*

montense and *P. glycyrrhiza* (both less than 24 μ long and averaging ca. 50 per mm^2). These differences are probably correlated with the tetraploid condition of *P. hesperium.*

Sorus shape, useful in separating the species, is not without some drawbacks. The sorus shape is often obscured in mature specimens by dehisced sporangia. In contrast sorus shape is usually quite clear in specimens with immature sporangia. *Polypodium glycyrrhiza* (fig. 5d) and *P. montense* (fig. 4b) usually have sori that are circular in outline while *P. hesperium* (fig. 3d) has larger oval sori.

The position of the sorus on the frond segment also is a useful character. In *P. glycyrrhiza* and *P. hesperium* the sori are located medially between the segment margin and the costa while in *P. montense* and *P. virginianum* they are located nearer the margin.

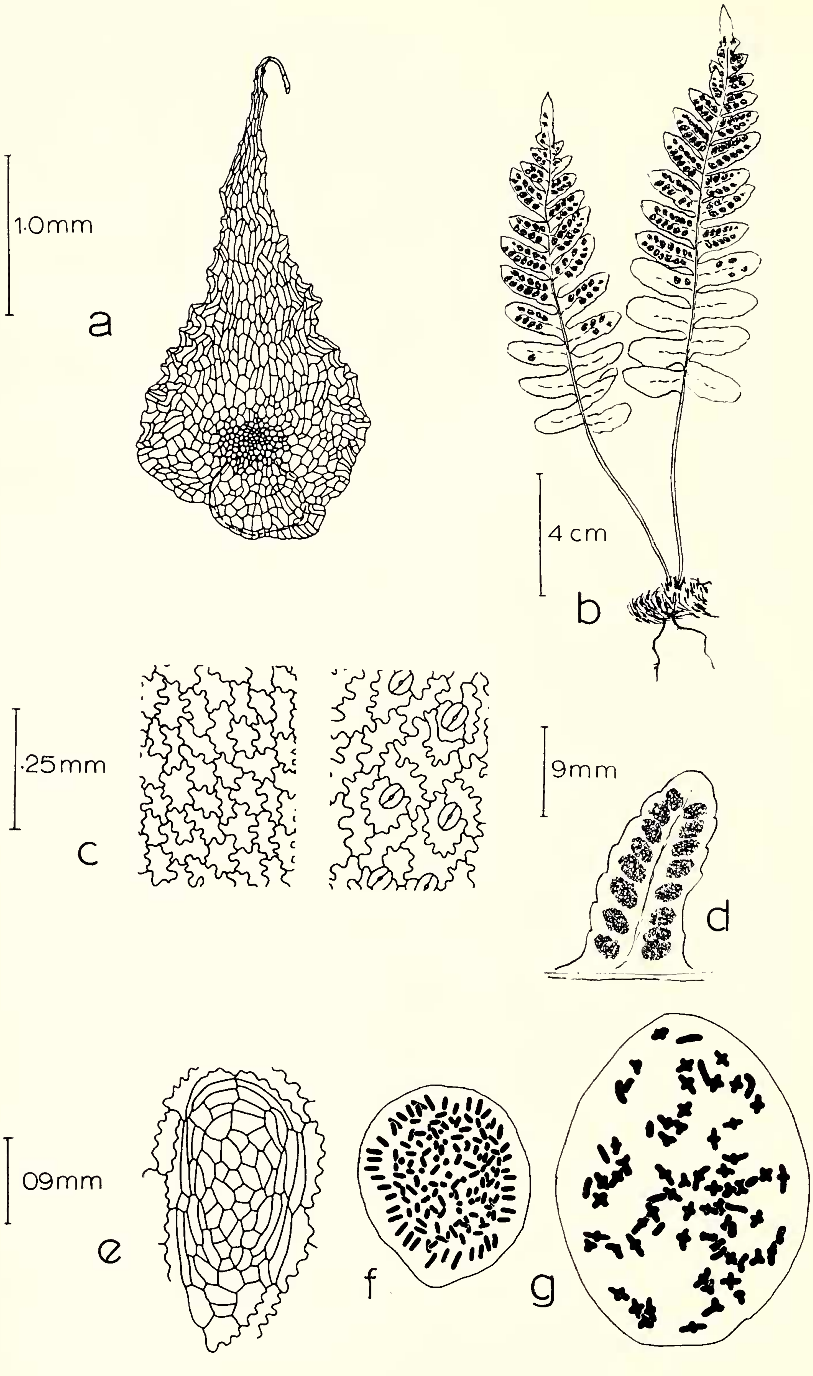
Shivas (1961a; 1961b) used the number of annular cells to distinguish the European species with considerable success. Counts of annular cells in Northwest taxa yielded no definite pattern, with sporangia from all species examined having between 12–14 cells per annulus.

One interesting morphological feature is the presence of paraphyses scattered among the sporangia of *P. montense* and *P. hesperium.* The paraphyses are commonly found in *P. montense,* but are very infrequent in *P. hesperium.* They are absent in *P. glycyrrhiza.* The paraphyses seem to be identical to those found in *P. virginianum* (Martens, 1950; Morton and Neidorf, 1954). A paraphysis from *P. montense* is shown in Fig. 4d.

In addition to cytological and morphological differences, the three Northwest taxa differ chemically as well. The rhizomes of *P. glycyrrhiza* and *P. hesperium* taste somewhat like licorice while *P. montense* (and *P. virginianum*) have an acrid taste. Fischer and Lynn (1933) investigated *P. glycyrrhiza* as a possible source of licorice and found that no glycyrrhizin (a compound found in true licorice, *Glycyrrhiza glabra,* that is fifty times sweeter than sugar) was present. They concluded that the licorice-like taste was due to a mixture of a glucoside which they called polypodin, some unidentified substances, and sucrose. The chemical composition of a plant sometimes can be determined by the taste of the rhizome.

Some of the characteristics of the rhizome scales are also helpful in distinguishing between the taxa of *Polypodium* in the Northwest (figs. 3a, 4a, 5a). In addition to differences in size and the degree of toothing on the margin of the scales, when compared to the other species, *P. montense* often has a distinctive dark median stripe down its center. This is invariable the case in *P. virginianum.* The median stripe is absent in *P. glycyrrhiza* and *P. hesperium.* Boborov (1964) used the nature of the rhizome scale as an important diagnostic characteristic in his analysis of the *Polypodium* species of the USSR.

In all three species the old fronds are shed during or shortly after the annual initiation of new fronds. The species produce new fronds at dif-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ferent times of the year and, as a consequence, meiosis occurs and the spores mature at different times.

New fronds are produced by *P. glycyrrhiza* from June onward. Most specimens seem to produce new fronds in late summer with meiosis occurring in the fall. Mature spores can be found throughout the fall and winter months. *Polypodium hesperium* produces new fronds throughout the summer with the first being initiated in May. Plants can be found in all stages of development during most of the summer. New fronds are usually produced by *P. montense* in April or May with the spores maturing in June, July, and August.

In any given region the majority of the plants of a particular species produce new fronds at about the same time. In most localities where the species are found together, there is usually a considerable interval between the initiation of fronds in each case. In the Fraser River Canyon of British Columbia, for example, *P. montense* produces new fronds several months before *P. glycyrrhiza* initiates them.

Variations in the time of initiation of new fronds can be related to different climatic conditions in different parts of the species ranges or to annual fluctuations in local climatic conditions. Plants of *P. glycyrrhiza* from the north coast of British Columbia tend to put up their fronds earlier than those on the south coast. This could be accounted for by differences in climatic conditions in the north.

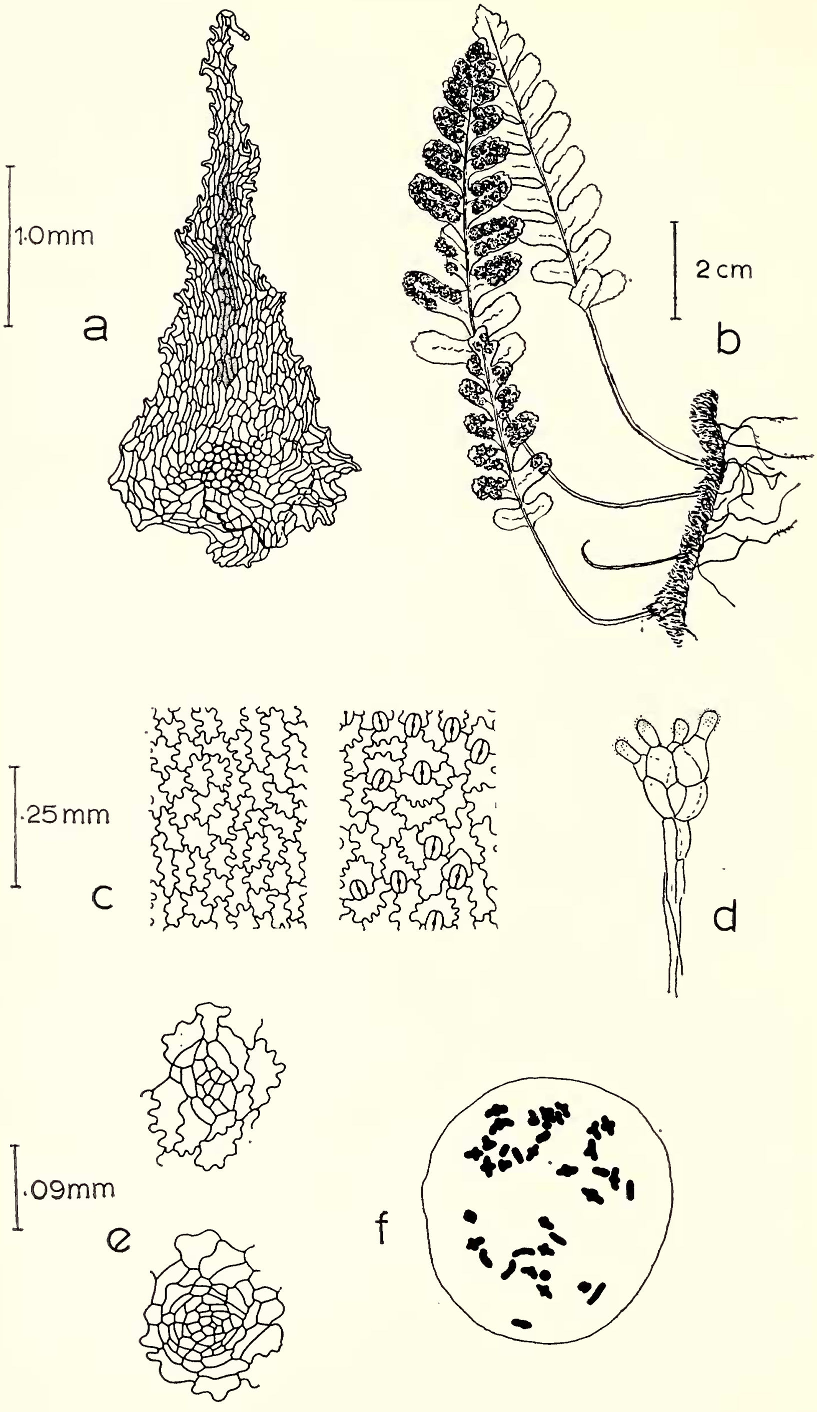
An example of an annual fluctuation of local climate affecting initiation of new fronds was noted in a population of *P. montense* from Mount Seymour, British Columbia. Cytological material was collected late in May 1962. The next spring material in the same condition could not be collected until almost a month later because the growing season was delayed by the late melting of the unusually heavy snowfall the preceding winter.

A map showing the distribution of these species in the Pacific Northwest has already been published (Lang. 1969).

SYSTEMATIC TREATMENT

When attempting to identify *Polypodium* species, difficulty is sometimes encountered when the specimen does not clearly show all of the diagnostic characteristics. For this reason a pragmatic key to the species is provided.

FIG. 3. Morphology and cytology of *Polydium hesperium:* a, rhizome scale, *Lang 212-C*; b, type specimen of *P. hesperium, M. W. Gorman 642*; c, upper and lower epidermal patterns, *Lang 74, Lang 111*; d, frond segment, note large oval sori, *Lang 111;* e, hydathode from upper epidermis, *Lang 71*; f, mitosis, **2n** = **148**, *Lang 201-A*; g, spore mother cell at diakinesis in *P. hesperium* from type locality, **n** = 74, *Lang 130–4.*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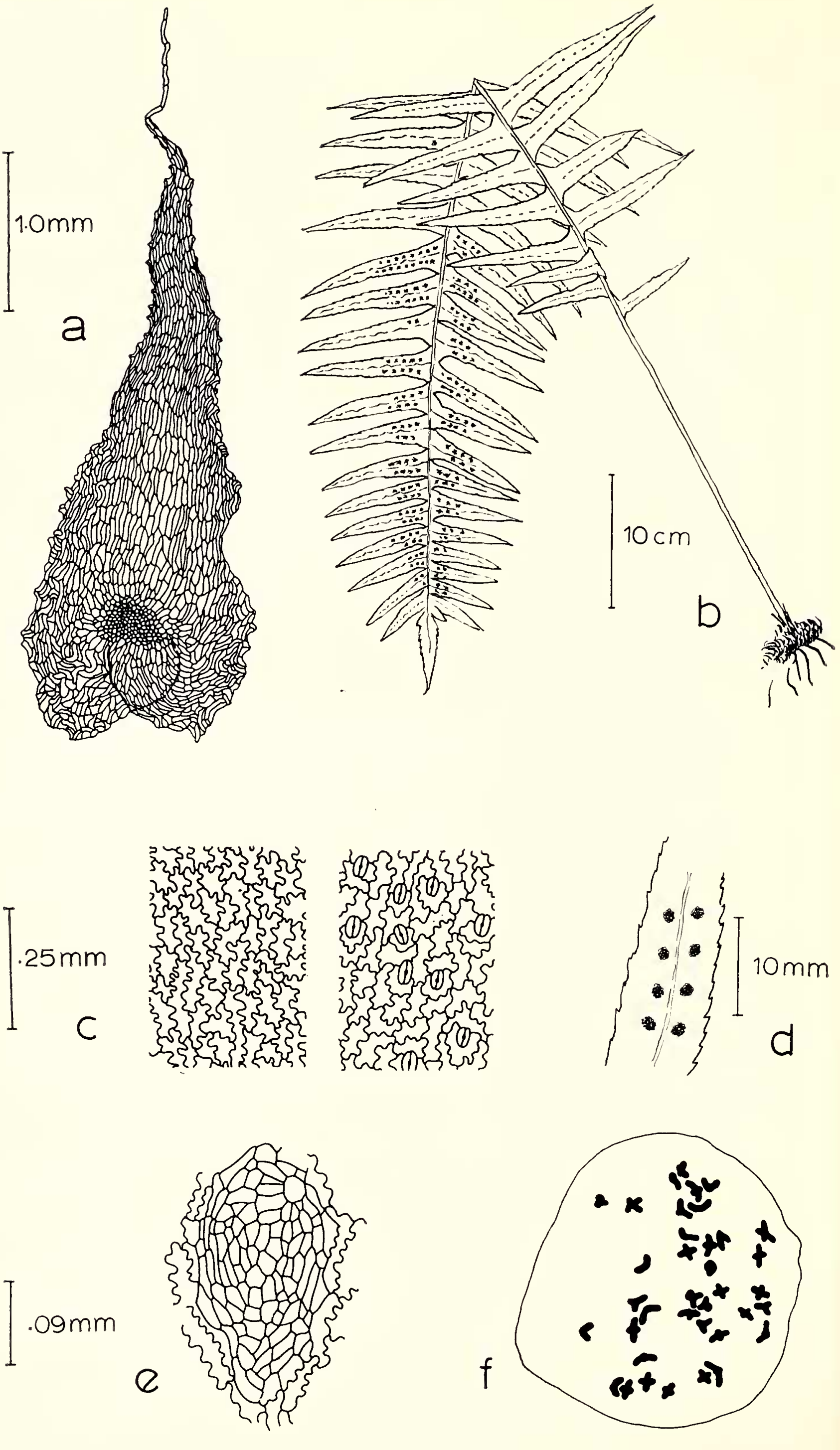
Key to the Species.

Polypodium virginianum and *scouleri* are included for completeness, but are not dealt with directly in this study.

- Paraphyses present.
  - Sori circular, submarginal; rhizome scales often with a median strike, coarsely toothed; rhizome acrid.
    - Frond segments narrowly ovate, mostly acute . . . . . 6. *P. virginianum*
    - Frond segments oblong to obovate, mostly obtuse . . . . . 2. *P. montense*
  - Sori oval, median; rhizome scales uniformly colored, not coarsely toothed; rhizome sweet.
    - Spores normal (not aborted) . . . . 1. *P. hesperium*
    - Spores aborted . . . . 5. *P. hesperium* × *montense*
- Paraphyses absent.
  - Sori circular.
    - Sori medial.
      - Frond segments usually more than 30 mm long, the ratio of length to width usually more than 3.3 (mean 5.6), acute to attenuate . 3. *P. glycyrrhiza*
      - Frond segments usually less than 30 mm long, the ratio of length to width usually less than 3.8 (mean 2.4), obtuse to acute.
        - Rhizome scales often with a median stripe, coarsely toothed; rhizome acrid, pruinose . . . . 2. *P. montense*
        - Rhizome scales uniformly colored, not coarsely toothed; rhizome sweet, not pruinose . . . . 1. *P. hesperium*
    - Sori submarginal . . . . 2. *P. montense*
  - Sori oval
    - Veins anastomosing . . . . *P. scouleri*
    - Veins free
      - Spores normal (not aborted).
        - Frond segments usually more than 30 mm long, the ratio of length to width usually more than 3.3 (mean 5.6), acute to attenuate. 3. *P. glycyrrhiza*
        - Frond segments usually less than 30 mm long, the ratio of length to width usually less than 3.8 (mean 2.4), obtuse to acute . . 1. *P. hesperium*
      - Spores aborted.
        - Segments entire to crenate, obtuse, the ratio of length to wides less than 2.0 . . . . 5. *P. hesperium* × *montense*
        - Segments serrate, acute, the ratio of length to width more than 2.0. 4. *P. glycyrrhiza* × *hesperium*

1. POLYPODIUM HESPERIUM Maxon, Proc. Biol. Soc. Wash. 13:200. 1900. *P. vulgare* L. var. *columbianum* Gilbert, List N. Amer. Pterid. 19, 38. 1901. *P. vulgare* L. var. *hesperium* (Maxon) Nelson & Macbride, Bot. Gaz. (Crawfordsville) 41:30 1916. *P. prolongilobum* Clute, Fern Bull. 18:97. 1910.

FIG. 4. Morphology and cytology of *Polypodium montense:* a, rhizome scale, *Lang 211-B*; b, habit, *Lang 211-B*; c, upper and lower epidermal patterns, *Lang 211-C*, *Lang 218*; d, paraphyses from sorus; e, hydathode from upper epidermis, *Lang 215*; and f, spore mother cell at diakenesis, n = 37, *Lang 189*.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Quantitative measurements are presented in the descriptions—manner to display variability. Using stipe length as an example the shortest stipe measured was (12 mm long) (80% of all stipes measured were from 28 to 100 mm long, the average stipe length being 57 mm long) (the longest stipe was 155 mm long). Quantitative data for *P. hesperium, P. montense* and *P. glycyrrhiza* are shown in Table 3.

Rhizome creeping, with sweet, licorice-like taste, 3–6 mm in diameter, paleaceous; rhizome scales tan to castaneus, ovate, to 5 mm long, somewhat crenate, the cells large, 25–30 in number across scale just above point of attachment; frond averaging 170 mm long, max. ca. 375 mm long; stipe stout, (12) (28–*57*–100) (155) mm long; blades coriaceous or herbaceous to membranous in shade, oblong (30) (163–*114*–189) (265) mm long, (12) (22–*33*–48) (83) mm wide; segments oblong, obtuse to acute, entire to serrate, (9) (11–*18*–26) (45) mm long, (5) (6–*7*–9) (11) mm wide, the ratio of length to width (1.3) (1.9–*2.4*–3.1) (3.8); hydathodes large, oval, many celled; veins free, forking 1–3 times; sori oval, located midway between costa and segment margin; paraphyses very rare; chromosome number **n = 74, 2n = 148.** Type. Coyote Canyon, Lake Chelan, Washington, *Gorman 642,* US!

New fronds produced from June to September; found growing on rocks and in rock crevices from south central British Columbia south to New Mexico, Arizona, and northern Mexico, east to the Rocky Mountains, west nearly to the coast in Cheakamus and Fraser River valleys of British Columbia, south along the east slope of the Cascade Mountains in Washington to Mount Hood, Oregon, absent from the Columbia Plateau in Washington, central Oregon, and the Great Basin region of Utah and Nevada, western limit of eastern [southerly] extension of range; eastern Washington, northwestern Oregon, Idaho, eastern Utah west of Zion Park in southern part of the state.

The reasons for the restriction of the epithet *hesperium* to the tetraploid cytotype have already been discussed (Lang, 1969).

Since the two cytotypes included in *P. hesperium* are recognized as two distinct species, it thus becomes necessary to establish to which cytotype the epithet *Hesperium* properly belongs, the diploid or the tetraploid. *Polypodium hesperium* Maxon is the oldest available name which must be used for one or the other of the two cytotypes.

The type specimen of *P. hesperium* was compared morphologically with a range of both diploid and tetraploid specimens from throughout the northwest and chromosome determinations were made on topotype material. This comparison makes it clear that the tetraploid cytotype agrees very closely with the type specimen of *P. hesperium* Maxon. Among other

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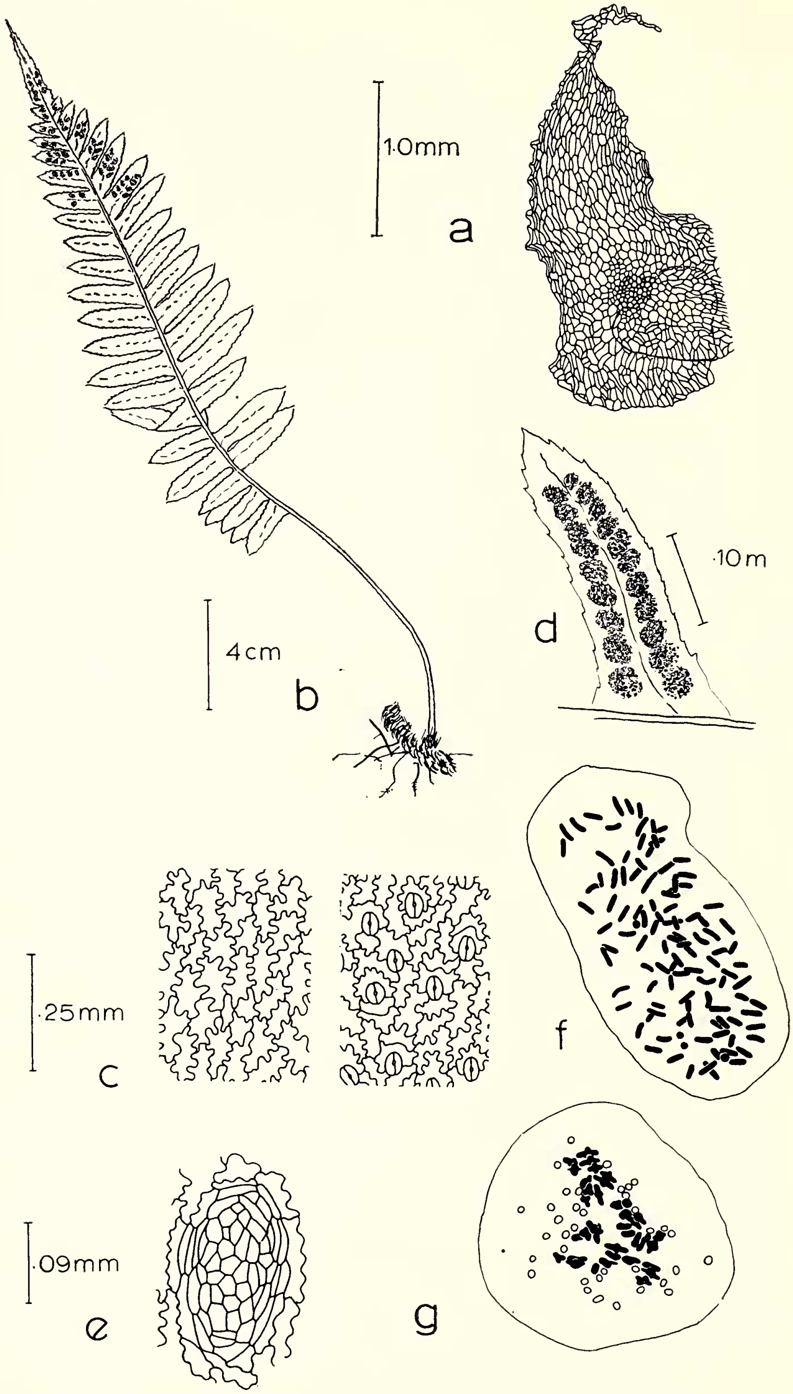
FIG. 5. Morphology and cytology of *Polypodium glycyrrhiza*: a, rhizome scale, *Lang 213*; b, habit, *Lang 189*; c, upper and lower epidermis, *Lang 33, Lang 217*; d, a portion of the frond segment of the type specimen of *P. glycyrrhiza*; note the round median sori; e, hydathode from upper epidermis, *Lang 24*; and f, spore mother cell at diakensis, n = 37, *Lang 189*.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g

features in common, both have oval sori located midway between the costa and segment margin, and a sweet licorice-like rhizome, as mentioned by Maxon (1900) in his original description. The diploid cytotype, on the other hand, has circular sori near the segment margin and an acrid flavored rhizome. The geographical distributions give further evidence that the holotype of *P. hesperium* is tetraploid since, as far as is known, the diploid cytotype does not occur in the same area as the tetraploid cytotype. A collecting trip to the type locality of *P. hesperium* in Coyote Canyon, Lake Chelan, Washington, yielded several isolated colonies of *Polypodium*. They were essentially similar in morphology, and all plants on which chromosome counts were made proved to be tetraploid. Figure 3g shows a spore mother cell from one of these plants at diakensis with 74 bivalents. On the basis of this evidence there is little doubt that the tetraploid should bear the name *P. hesperium* Maxon.

2. POLYPODIUM MONTENSE F. A. Lang, Madroño 20:57. 1969. *P. amorphum* Suksdorf, Werdenda 1:16, 1927. Holotype: Dog Creek Canyon, near Cooks, Skamania Co., Washington, *Suksdorf 11667,* WS.

Rhizome creeping, acrid, 3–5 mm in diameter, ofter pruinose, paleaceous; rhizome scales dark brown to castaneus, often with a central strip of darkly colored cells, narrowly ovate to obovate, often constricted above point of attachment, to 5 mm long, usually with a capillary tip, margin coarsely toothed, cells large, ca. 25 in number across scale just above point of attachment; frond averaging 130 mm long; max. ca. 300 mm long; stipe slender, (8) (28–*58*–100) (142) mm long; blades coriaceous to membraneous, oblong (18) (46–*81*–122) (190) mm long, (11) (17–*24*–30) (45) mm wide; segments oblong to obovate, tips obtuse to rarely acute, entire to crenulate, (5) (9–*13*–17) (25 mm long, (3) (4–*6*–7) (12) mm wide, ratio of length to width (1.2) (1.8–*2.3*–3.0) (3.6); hydathodes small, round, few-celled; veins free, forking 1–2 times; sori circular, nearer the margin than the costa; paraphyses many; chromosome number **n = 37, 2n = 74.** Holotype. Creakamus River, British Columbia, *Lang 211,* UBC.

New fronds produced from late April to June; found growing in rock crevices in mountains from central Coast Range in British Columbia south through the Cascade Mountains in Washington to Oregon and the Sierra Nevada Range in California, in the Olympic Mountains and Wenatchee Mountains of Washington and the Northern Coast Range of Oregon, usually at high elevations but descending to bottoms of river valleys.

FIG. 6. Morphology and cytology of *Polypodium glycyrrhiza* × *hesperium*: a, rhizome scale, *Lang 210-C*; b, habit, *Lang 210-C*; c, upper and lower epidermal patterns, *Lang 210-C, Lang 125–2*; d, frond segment, note large oval sori, *Lang 210-C*; e, hydathode from upper epidermis, *Lang 210-C*; f, mitosis, **2n = 111**, *Lang 125–2*; and g, spore mother cell at metaphase I, $37_{II} + 37_{I}$, *Lang 125–2.*

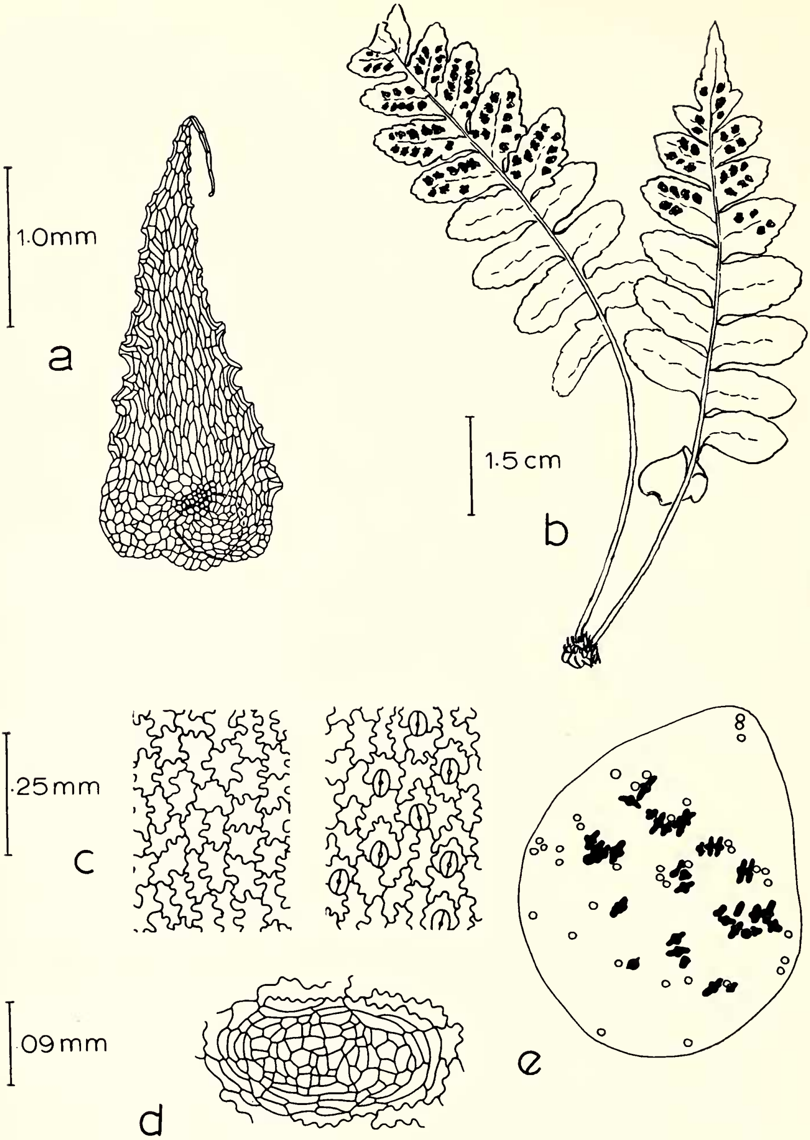

FIG. 7. Morphology and cytology of *Polypodium hesperium* × *montense*: a, rhizome scale, *Lang 122–3*; b, habit, *Lang 122–3*; c, upper and lower epidermal patterns, *Lang 122–3*; d, hydathode from upper epidermis, *Lang 122–3*; and e, spore mother cell at metaphase I, $37_{\mathrm{II}} + 37_{\mathrm{I}}$, *Lang 122–3*.

A discussion, treatment, and description of this taxon has already appeared (Lang, 1969).

3. Polypodium glycyrrhiza D. C. Eaton, Amer. J. Sci II. 22:138. 1856. *P. vulgare* L. var. *occidentale* Hook., Fl. Bor. Amer. 2:258. 1840. *P. falcatum* Kellogg, Proc. Calif. Acad. Sci. 1:20. 1854. Non L. fil. Suppl. 446. 1781. *P. vulgare* var. *rotundatum* Milde, Fil. Europ. Atlant. 18. 1867. *P. vulgare* var. *falcatum* (Kellogg) Christ. Beitr. Krypt. Schweiz. 2:51. 1900. *P. occidentale* (Hook.) Maxon, Fern Bull. 12:102. 1904. *P. vulgare* subsp. *occidentale* (Hook.) Hulten, Acta Univ. Lund. 37:44. 1941. *P. aleuticum* A. Bobr. Bot. Zhur. (Moscow & Leningrad) 49:542. 1964.

Rhizome creeping, sweet, with licorice-like taste, 3–6 mm in diameter, pleaceous; rhizome scales narrowly ovate to ovate, up to 10 mm long, tan to castaneus, uniformly colored, more or less entire, sometimes with a prolonged capillary tip, the cells small, about 40 in number across scale just above point of attachment; frond averaging 260 mm long (max. ca. 600 mm) stipes stout, (11) (36–*94*–143) (340) mm long; blades subcoriaceous on exposed rock, herbaceous or membraneous in shade, oblong to ovate, sometimes deltoid, (20) (69–*173*–280) (470) mm long, (14) (35–*60*–92) (156) mm wide; blade segments narrowly oblong-attenuate, more or less falcate, acute to acuminate, (7) (18–*33*–53) (85) mm long, (3) (5–*7*-8) (11) mm wide, the ratio of length to width (1.8) (3.3–*5.6*–7.4) (12.0); hydathodes large, oval, many celled; veins free, forking 2–4 times, sori usually circular, sometimes slightly oval, located midway between costa and margin; paraphyses absent; chromosome number **n = 37, 2n = 74.** Type. Port Orford, Kuntz s.n., YU!

New fronds produced from August to February; found growing at lower elevations on rocks and trees along the Aleutian Islands to Alaska, south through coastal British Columbia, Washington, Oregon and California to Monterey Co.; east to the Cascade Mountains in the southern part of the range and extending up inlets and river valleys in the coastal mountains of British Columbia.

There is no doubt that the correct name of the coastal diploid species is *P. glycyrrhiza* D. C. Eaton since this epithet has priority over the others. Two varieties of *P. glycyrrhiza* might be recognized on the basis of frond segment shape, one with attenuate frond segments, the other with acute to subobtuse segments.

The forms with attenuate frond segments have been recognized as *Polypodium vulgare* var. *occidentale* Hook., and it is possible that *P. vulgare* var. *rotundatum* Milde would include the acute to subobtuse forms. However, new combinations of these parieties in *P. glycyrrhiza* should be delayed until the precise relationship of the two forms has been intensively studied.

4. Polypodium glycyrrhiza × hesperium.

Because of the few plants that were examined, no formal characterization of this and the following triploid hybrid is attempted. The major morphological characteristics are shown in Fig. 6.

Specimens examined. BRITISH COLUMBIA: Kaske Creek, 59 miles E of Prince Rupert, *Lang 99-B,* UBC; Alexandra Bridge, Fraser River, *Lang 125–2,* UBC; Green River, Pemberton, *Lang 210–C,* UBC.

5. Polypodium hesperium × montense.

Figure 7 is of the only known triploid of this parentage.

Specimen examined. BRITISH COLUMBIA: Alexandra Bridge, Fraser River, *Lang 122–3,* UCB.

6. Polypodium virginianum.

Several specimens of *P. virginianum* from northeastern British Columbia and the Yukon were examined because of their close proximity to the study area.

The Origin of Polypodium hesperium

In view of the available evidence a tentative hypothesis may be made concerning the origin of the tetraploid *P. hesperium.* It seems likely that *P. hesperium* is an allotetraploid that arose from the diploids *P. glycyrrhiza* and *P. montense* or their progenitors. Comparison of *P. hesperium* (fig. 3) and the two diploids (figs. 4 and 5) indicate that *P. hesperium* is more or less morphologically intermediate between them. The fact that *P. hesperium* invariably forms 74 bivalent chromosomes (no multivalents) at meiosis is further evidence of its alloploid origin.

Perhaps the most convincing evidence is offered by morphology and the meiotic chromosome behavior of the two triploid hybrids, *P. hesperium × montense* and *P. glycyrrhiza × hesperium.* By comparing the specimens in Figs. 6 and 7, it is clear that there are two morphologically distinct triploid hybrids. Because they have 111 sporophytic chromosomes, they must have been derived from hybridization between a tetraploid with 74 gametic chromosomes and a diploid with 37 gametic chromosomes. The fact that the tetraploid *P. hesperium* and the two diploids, *P. glycyrrhiza* and *P. montense,* are the only species known from the region where the triploids were found is sufficient basis to suspect them as being the parental species. Each triploid probably shared *P. hesperium* as a common parent since it is the only available tetraploid. The two triploids are more or less intermediate between *P. hesperium* and *P. glycyrrhiza* in one case (compare figs. 3, 5, 6), and *P. hesperium* and *P. montense* in the other (figs. 3, 4, 7). It seems that these species are the parents of the hybrids. At meiosis these morphologically distinct triploids both show $37_{II} + 37_{I}$ chromosomes. This indicates that both the *P. glycyrrhiza* genome and the *P. montense* genome are present in *P. hesperium* if we assume that the pairing is due to genome homology and not some other mechanism. Following the convention of Shivas (1961a), we can assign letters to the genomes of the different species to illustrate what might be occurring at meiosis in the triploid hybrids. *Polypodium glycyrrhiza,* a diploid, possesses sets of homologous chromosomes represented

AA, while *P. montense* has a different set of homologous chromosomes DD (B and C were used by Shivas for other members of the complex). When the gametes from *P. hesperium,* which are diploid, combine with a haploid gamete from one of the diploids, a triploid will result. When meiosis occurs in this triploid, $37_{II} + 37_{I}$ form. If the tetraploid is indeed an allotetraploid derived from *P. glycyrrhiza* and *P. montense,* then one could expect that it would have genomes AA and DD. This assumption is borne out by chromosome pairing in the triploid. In *P. glycyrrhiza* × *hesperium* we find $37_{II} + 37_{I}$, AA + D. The A genome from the *P. glycyrrhiza* gamete is pairing with A genome present in the *P. hesperium* gamete with the *P. montense* genome unpaired. The reverse is true for *P. hesperium* × *montense.* The two DD genomes pair while the single A genome o*f P. glycyrrhiza* with 37 chromosomes remains unpaired. From the abortive nature of the spores of the triploid, it seems likely that fertility is greatly reduced in them and that *P. hesperium* is reproductively isolated from the two diploids. It is interesting to note that no hybrids between the diploid cytotypes have been found in nature or have been synthesized in culture. *Polypodium glycyrrhiza* and *P. montense* are occasionally found growing so close together that their rhizomes are intertwined, yet there seems to be no sign of any diploid hybrids.

On the basis of chromosome pairing in these triploids, it appears that both the genomes of *P. glycyrrhiza* and *P. montense* are present in the tetraploid *P. hesperium* .Of course, this is only a tentative conclusion based on the available evidence. Before any definite conclusions are reached concerning the origin of *P. hesperium,* the parentage of the triploids should be confirmed by synthesized hybrids and crosses established between *P. hesperium* and all the diploid members of the complex.

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Literature Cited

Blasdell, R. F. 1963. A monographic study of the fern genus Cystopteris. Mem. Torr. Bot. Club 21(4):1–102.

Boborov, A. E. 1964. A comparative morphological and taxonomical study of the species of Polypodium L. of the flora of the U.S.S.R. Bot. Zurn. (Moscow & Leningrad) 49:534–545.

Evans, A. M. 1963. New chromosome observations in the Polypodiaceae and Grammitidaceae. Carylologia 16:671–677.

————., and W. H. Wagner, Jr. 1964. Dryopteris goldiana × intermedia—a natural woodfern cross of noteworthy morphology. Rhodora 66:255–266.

Fischer, L., and E. V. Lynn. 1933. Licorice fern and wild licorice as substitutes for licorice. J. Amer. Pharm. Assoc. 22:1225.

Knobloch, I. W. 1962. Tetroploid Polypodium vulgare var. columbianum from Arizona. Amer. Fern J. 52:65–68.

Lang, F. A. 1965. A cytotaxonomic study of the Polypodium vulgare complex in Northwestern North America. Ph.D. thesis, University of British Columbia.

————. 1969. A new name for a species of Polypodium from northwestern North America. Madroño 20:53–60. 1959.

Lloyd, R. M. 1962. Studies in California species of Polypodium (Polypodiaceae) Master's thesis. Claremont Graduate School.

————. 1963. New chromosome numbers in Polypodium. Amer. Fern. J. 53:99–101.

————., and F. A. Lang. 1964. The Polypodium vulgare complex in North America. Brit. Fern Gaz. 9:168–177.

Manton, I. 1950. Problems of cytology and evolution in the pteridophyta. Cambridge University Press.

Martens, P. 1950. Les organes glanduleux de Polypodium virginianum III. Nouvelles donnees géographiques, systematiques et histologiques. La Cuellule. 53:187–212.

Morton, C. V., and C. Neidorf. 1954. Polypodium vulgare var. virginianum. Amer. Fern J. 44:111–114.

Shivas, M. G. 1961a. Polypodium in Europe and America. I. Cytology. J. Linn. Soc., Bot. 58:27–38.

————. 1961b. Polypodium in Europe and America. II. Taxonomy. J. Linn. Soc., Bot. 58:27–38.

Taylor, T.M.C. 1970. Pacific Northwest ferns and their allies. Univ. Toronto Press, Toronto.

Wagner, W. H. Jr. 1954. Reticulate evolution in Appalachian aspleniums. Evolution 8:103–118.

————., and L. L. Chen. 1965. Abortion of spores and sporangia as a tool in the detection of Drypteris hybrids. Amer. Fern Jr. 55:9–29.

LOCAL PHOTOSYNTHETIC ECOTYPES IN PINUS ATTENUATA AS RELATED TO ALTITUDE

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This paper reports ecotypic varation in *Pinus attenuata* Lemm., as determined by temperature conditioning in greenhouse-grown seedlings from seed collected at the elevational extremes of its range in the San Bernardino Mountains of southern California.

Although most genecological studies are on wide ranging species, a number of instances of localized variability have been published. Culberson and Culberson (1967) found local ecological sorting of a lichen species on a coastal promontory in North Wales. Briggs (1962) demonstrated a mosaic of local ecotypes of a *Ranunculus* species. Squillace and Bingham (1958) showed localized ecotypic variation in western white pine, related to elevation, slope direction and soil moisture. The work of Kruckeberg (1968) has demonstrated many ecotypes related to narrowly restricted edaphic conditions.

Local ecotypes or ecoclines related to altitude have also been found. Papers from the Carnegie group, typified by Clausen, Keck, and Hiesey (1948) involve altitude as a principal habitat gradient. Other geneco-